

A SYNOPSIS OF THE GENUS *CLUSIA* SECTIONS *CRIUVOPSIS* AND *BRACHYSTEMON* (CLUSIACEAE) IN NORTHERN SOUTH AMERICA

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ABSTRACT

The genus *Clusia* sections *Criuvopsis* and *Brachystemon* are revised, in preparation for a treatment of the Clusiaceae for *Flora of the Venezuelan Guayana* and *Flora de Colombia*. Amplified descriptions, keys to the species and lectotypifications are provided for each section. In *Clusia* section *Criuvopsis*, 3 species are recognized, of which one, *Clusia araracuarae*, is described as new, illustrated, and its phylogenetic relationships discussed. Amplified descriptions, illustrations and discussions of phylogenetic relationships are provided for *Clusia amazonica* and *C. martiana*. *Clusia oedematopoidea* is reduced to synonymy under *C. amazonica*, and *C. uleana* under *C. martiana*. In *Clusia* section *Brachystemon*, 3 taxa are recognized, of which one, *Clusia aymardii*, is described as new, illustrated, and its phylogenetic relationships are discussed. Amplified descriptions and discussions of phylogenetic relationships are provided for *Clusia spathulaefolia* and *C. penduliflora*.

RESUMEN

Como resultado de investigaciones para preparar un tratamiento taxonómico del género *Clusia* para *Flora of the Venezuelan Guayana* y *Flora de Colombia*, se presenta una revisión de las secciones *Criuvopsis* y *Brachystemon*. Se presentan descripciones actualizadas para las dos secciones, claves para separar sus especies, y se lectotipifican. Se reconoce tres especies en la sección *Criuvopsis*, entre las cuales, *C. araracuare*, se describe como especie nueva, se ilustra, y se discute su parentesco. Se provee descripciones ampliadas, ilustraciones y comentarios sobre relaciones filogenéticas para *Clusia amazonica*, y *C. martiana*. Se relega *C. oedematopoidea* a sinonimia bajo *C. amazonica* y, a *C. uleana* bajo *C. martiana*. In sección *Brachystemon*, se reconoce tres especies, entre las cuales, *C. aymardii* se describe como especie nueva, se ilustra, y se discute su parentesco. También, se provee descripciones ampliadas, y comentarios sobre relaciones filogenéticas para *C. spathulaefolia* y *C. penduliflora*.

INTRODUCTION

The genus *Clusia* Linnaeus contains over 250 species (with 336 names), distributed throughout the Neotropics, with two, *C. rosea* Jacquin, and *C. minor* Linnaeus, widely cultivated throughout the tropics. Despite taxo-

nomic overdescription, it is estimated that there are at least an additional 40 as yet undescribed species in the Andes of Colombia, Ecuador, Peru and Bolivia, particularly in the premontane, montane (including ceja de selva), subpáramo, páramo and jalca habitats. The genus is easily recognized by its capsular, septicidally dehiscent fruits, with few to numerous stamens, and copious cream, yellow or white latex. Characters traditionally used to define the sections of the genus include the structure of the androecium in stamineate flowers, and corresponding structure of the stigmas and staminodes of the pistillate. The last comprehensive revision was that of Vesque (1893), in which Engler's (1888) classification was simplified. The taxonomy of the group is difficult owing to its sexual lability, with stamineate, pistillate, bisexual (Hammel 1986) and apomictic (Hammel 1986; Maguire 1976) individuals known. In addition, I have seen stamineate flowers on reiterative (sensu Hallé et al. 1978) shoots of otherwise functionally pistillate plants in *Clusia pusilla* Steyermark and in *C. grandiflora* Splitgerber, in the Pakaraima Mountains of Guyana and on the Chimantá Massif complex of tepuis in the eastern portion of the state of Bolívar, Venezuela.

While preparing a diagnostic treatment of the genus for the *Flora of the Venezuelan Guayana* and a more comprehensive one for *Flora de Colombia*, sections *Criuvopsis* and *Brachystemon* were revised. These two sections form a natural group, closely related to section *Criuva* Benth. Engler (1893) considered both sections *Criuvopsis* and *Brachystemon* to be subsections within subgenus *Criuva* sensu Benth (1862). In fact, this study grew out of the difficulty in distinguishing young plants of *Clusia (Brachystemon) penduliflora* from *C. (Criuvopsis) martiana*. Because the formats of the floristic treatments in preparation do not allow for complete descriptions and synonymy, the present treatment is intended to provide data for the groups over their entire range, until a more comprehensive revision is prepared.

TAXONOMIC TREATMENT

Clusia L. section Criuvopsis Planchon and Triana, Ann. Sci. Nat., Ser. 4 13:322. 1860. LECTOTYPE SPECIES (here designated): *Clusia amazonica* Planchon and Triana, Ann. Sci. Nat., Ser. 4 13:358. 1860.

Clusia section *Criuva* Bentham and Hooker, subsection *Criuvopsis* (Planchon and Triana) Engler, Fl. Bras. 12(1):401. 1888. J. Vesque in A. DC and DC, Monogr. Phan. 8:77. 1893.

Clusia subgenus *Criuva* (Bentham and Hooker) Engler, section *Criuvopsis* (Planchon and Triana) Engler, Nat. Pflanzenfam. 3(6):225. 1895.

Glabrous lianas or hemiepiphytes; latex white to translucent. Leaves petiolate. Inflorescence a terminal panicle, the flowers cymose; secondary inflorescence bracts 2, coriaceous; bracteoles 4, decussate, coriaceous. Perianth spreading; sepals 4–5, chartaceous, opposite the petals; petals 5, contorted,

very thickly carnose; androphore pentagonal, stamens numerous, the filaments short, flat, apically free, connate at the base, fleshy, often thickened at the base; anthers basifix, muticous, equaling or slightly longer than the filaments, truncate to emarginate apically, dehiscent by longitudinal slits; pistillode absent, the central receptacle resiniferous or not. Pistillate inflorescence and flowers as in staminate, but staminodia 5, free, linear, with vestigial anthers; carpels 5, stigmas thin, elliptic to oblong, peltate; ovules horizontally ascending;. Fruit a capsule, ovoid to oblongoid, stigma and styles persistent.

Distribution.—Three species, distributed from Panama to Colombia, Venezuela, Ecuador, Peru, Bolivia and Amazonian Brazil.

Clusia section *Criuvopsis* appears to be most closely related to *C.* section *Brachystemon* by virtue of its short, thick filaments of the fertile stamens, sessile stigmas, and linear anthers dehiscent by longitudinal slits. However, section *Criuvopsis* may be easily distinguished from section *Brachystemon* by the flat filaments connate basally, and very thin inflorescence rachises.

KEY TO SPECIES OF *CLUSIA* SECTION *CRIUVOPSIS*

1. Leaf blades oblong, bullate; sepals 4; petals 5; anthers rounded to slightly emarginate apically and basally 1. *C. araracuarae*
1. Leaf blades obovate to elliptic, smooth; sepals 5, petals 5; anthers muticous.
 2. Leaf base obtuse to broadly rounded, leaves coriaceous, adaxial latex canals inconspicuous, adaxial venation and submarginal collecting vein prominent; liana. 2. *C. amazonica*
 2. Leaf base acute to cuneate, leaves subcoriaceous, adaxial latex canals highly conspicuous, adaxial venation inconspicuous, submarginal collecting vein barely discernible; scandent, epiphytic shrub, at times appearing lianous 3. *C. martiana*

1. *Clusia araracuarae* Pipoly, sp. nov. (Fig. 1)

Propter lamina coriacea ad bases obtusa vel late rotundata, nervos secundarios conspicuous necnon nervo submarginale conjunctos, *C. amazonicae* valde arcte affinis, sed ab ea laminis oblongis (non obovatis vel ellipticis), necnon bullatis (nec laevibus), sepalis 4 (non 5), tandem antheris ad apices basesque emarginatis vel rotundatis (non muticis), praecclare distat.

Scandent lianous shrub, to 23 m long, 4 cm diam. glabrous; branchlets tetragonal in cross section, squarrose, 3–5 mm diam., bark of apical portions rufous, appearing scaly, checking transversely, gray at maturity, rugose, latex white, copious. Leaves decussate; blades coriaceous, oblong, (8)13–18 cm long, (2.5–)3–3.5(–4) cm wide, apex abruptly acuminate to rostrate, base widely rounded to truncate, deeply bullate, nitid above at first, then pallid above and below at maturity, midrib deeply impressed above, prominently raised below, secondary veins 17–32 pairs, perpendicular to midrib, deeply impressed above, prominently raised below, united by a prominent

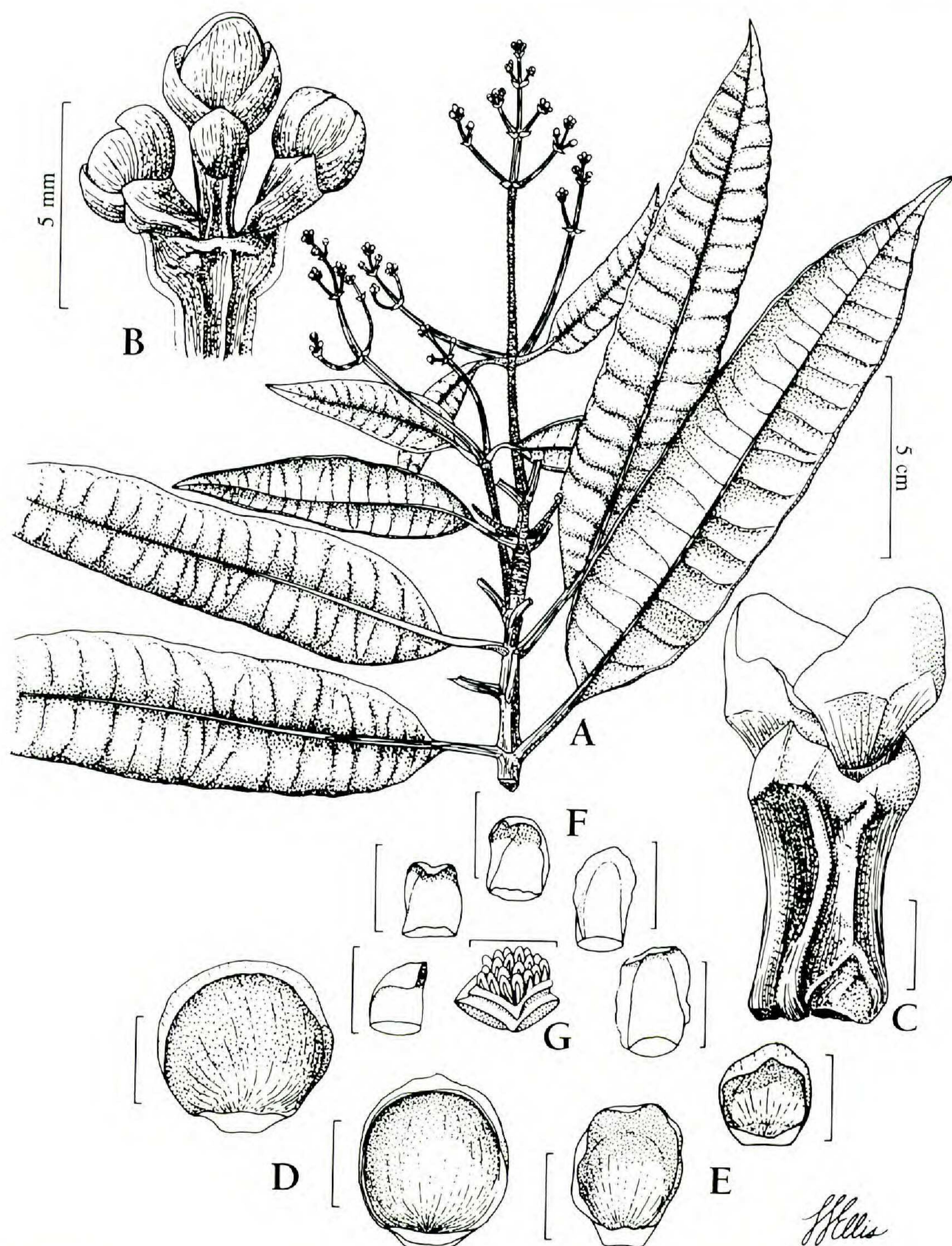


FIG. 1. *Clusia araracuarae* Pipoly. A. Habit, showing the oblong, bullate leaves. B. Closeup of cyme, showing callose keels of bracteoles. C. Quadrate pedicel. D. Outer sepals. E. Inner sepals. F. Petals. G. Androecium, showing pentagonal morphology and apically rounded anthers. A–G, drawn from holotype.

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submarginal collecting vein, latex canals linear, conspicuous, margin revolute, entire; petioles deeply canaliculate, 2.5–2.8 mm long, glabrous. Stamineate inflorescence terminal, erect, pyramidally paniculate, 7–9 cm long and 5–7 cm wide in bud, the branches cymose, flowers in 3's; peduncle 3.5–5 cm long, subtended by two reduced leaves similar to vegetative leaves but 3–5 cm long, 1.4–1.8 cm wide; secondary inflorescence bracts carnose, depressed-ovate, 1.3–1.6 mm long, 1.6–1.8 mm wide, apex rounded, medially carinate, the margin opaque, not scarious, entire; pedicel squarrose, 2.8–4.2 mm long; bracteoles four, 2 decussate pairs, carnose, depressed-ovate to suborbicular, apex obtuse, carinate medially, the keel callose, hyaline, the margin entire, glabrous, the outer 2–2.5 mm long, 2.3–2.6 mm wide, the inner 2.5–3 mm long and wide. Stamineate flower buds cream; outer sepals 2, opposite, coriaceous, orbicular, 2.3–6 mm long and wide, apex very widely rounded, cucullate, hyaline except apically, the margin entire; inner sepals 2, decussate to the outer ones, coriaceous, as outer sepals but reddish, hyaline apically; petals 5, contorted, carnose, oblong, 0.8–1.1 mm long, 0.4–0.6 mm wide in bud; androphore convex, pentagonal as seen from above; stamens numerous, 0.9–1 mm high, the filaments flat, 0.6–0.8 mm long, the anthers linear, 0.1–0.2 mm long, emarginate or rounded apically and basally; pistillode absent, not resiniferous. Pistillate inflorescence unknown. Fruit unknown.

TYPE: COLOMBIA. AMAZONAS: Araracuara, along Río Caquetá, right bank, 3 km above Sumaeta, 0°36'S, 72°10'W, riparian floodplain, 200–300 m, 30 Sep 1990 (stam. fl bud), E. Alvarez, A.C. Londoño, A. Rodríguez, & F. Moreno 116 (HOLOTYPE: COAH!; ISOTYPE: NY!).

Distribution.—Known only from the type.

Ecology and conservation status.—*Clusia araracuarae* occurs in Igapó vegetation (Prance 1979), forming mats in canopies of trees along black water river margins. The area in which this species occurs is subject to extreme disturbance owing to forest destruction, largely for firewood. Araracuara is a significant population center and busy port on the Río Caquetá, and therefore, this species should be considered threatened.

The long inflorescences, lianous habit, leaves with prominent secondary venation and submarginal collecting vein and obtuse to broadly rounded bases, indicate that *Clusia araracuarae* is most closely related to *Clusia amazonica*. However, the bullate leaf blades, fewer sepals, and anthers that are rounded to emarginate apically and basally clearly set *C. araracuarae* apart.

2. *Clusia amazonica* Planchon and Triana, Ann. Sci. Nat., Ser. 4 13:358. 1860. (Fig. 2). TYPE. BRAZIL. AMAZONAS: near Panure along the Rio Uaupes, Oct 1852–Jan 1853 (stam. fl), R. Spruce 2878 (HOLOTYPE: P!; NY Neg. 5033; ISOTYPE: P!; NY Neg. 5034).

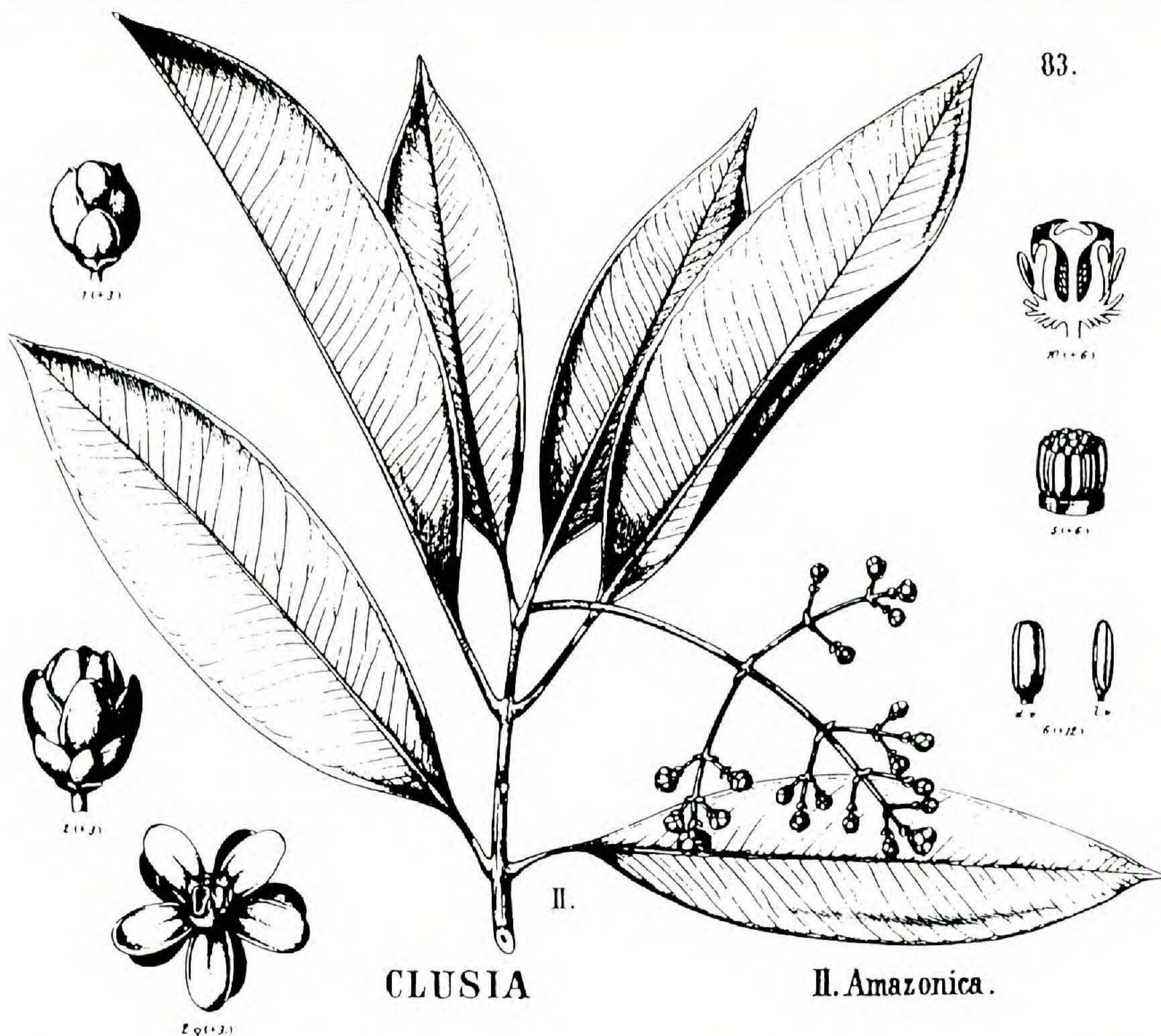


FIG. 2. *Clusia amazonica* Planchon et Triana. Habit (center); staminate bud, pistillate flower bud, pistillate flower, stamens in abaxial and lateral views, androecium, and longisection through pistillate flower (counterclockwise, from upper left). Adapted from Engler in Martius, *Flora Brasiliensis*, 12: Plate 83.

Clusia oedematopoidea Maguire, Phytologia 39:73. 1978. TYPE. PANAMA. PANAMA: J. Duke 13557 (HOLOTYPE: NY; ISOTYPE: MO!).

Liana; branchlets tetragonal in cross section, squarrose, (2.5–)3–5.5(–7) mm diam., bark of apical portions rufous, appearing scaly, checking transversely and exfoliate, beige at maturity, rugose; latex white, copious. Leaves decussate; blades coriaceous, oblong, elliptic or rarely obovate, (8.0–)10.5–20.0(–26.0) cm long, (3.5–)4.0–4.6–10.5(–12.2) cm wide, apex broadly rounded, with an abruptly short-acuminate tip, the acumen 0.5–1 cm, base obtuse to broadly rounded, not decurrent on the petiole, smooth, sordid above, pallid below, latex canals varying in conspicuousness above, but never readily visible without magnification below, midrib prominently raised above and below, secondary veins numerous, prominently raised above, slightly raised below, united by a fine submarginal collecting vein, the mar-

gin subrevolute, entire, glabrous; petioles canaliculate, (2.1–)2.7–4.0 (–5.8) cm long. Inflorescence terminal, erect, pyramidal paniculate, (6–) 12–24 cm long, 6–10 cm wide at maturity, the flowers cymose, 3 per cyme; peduncle (2–)4–8(–11.5) cm long, subtended by normal leaves; secondary bracts coriaceous, very widely ovate, 1.5–2.5 mm long, 1.5–2 mm wide, apex obtuse to rounded, carinate, the margin hyaline, scarious, entire. Stamine inflorescence with tetragonal pedicels, 3–5 mm long; bracteoles 4, decussate, the outer 2 coriaceous, very widely ovate, 1.5–2.5 mm long, 1.5–2 mm wide, apex obtuse to rounded, carinate, the margin hyaline, scarious, entire, the inner 2 suborbicular to orbicular, 2.5–3 cm long and wide, apex rounded, flat, the margins entire, hyaline, scarious. Stamine flowers white; sepals 5, contorted, membranaceous, brittle, suborbicular to orbicular, 5–6 mm long and wide, apex broadly rounded, translucent, densely lineate, the margin hyaline, scarious; petals 5, contorted, carnose, somewhat cucullate, oblong, 3.5–4 mm long, 2.5–3 mm wide, apex obtuse to rounded, somewhat cucullate, densely lineate, the margin hyaline; androphore flat or slightly concave, pentagonal, the stamens numerous, free, 2.5–3.5(–3.7) mm long at maturity, the filaments short, flattened, ca. 1–1.2 mm long, the anthers linear, 1.5–2.5 mm long, 0.7–1 mm wide, apex truncate, base truncate, dehiscent by wide longitudinal slits, abruptly expanding at base to filament, the connective flat, darkened; pistillode obsolete, resin scanty. Pistillate inflorescence as in stamine but (1.5–)2–3(–5) mm long; outer bracteoles deltate, 1.8–2 mm long and wide; inner bracteoles oblate, 2.7–3.5 mm long, 3–3.7 mm wide. Pistillate flowers white, as in stamine but sepals orbicular, 6–7 mm long and wide; petals strongly cucullate, 6–6.5 mm long, 3.5–4 mm wide, staminodes 5, flat, 2.5–3.5 mm long, the filament ca. 1 mm long, abruptly tapering at apex, the anther linear, ca. 1.5–2.5 mm long, apex broadly rounded, not well-differentiated from apex of filament, the thecae not fully differentiated and devoid of pollen, the connective darkened; pistil 3–5 mm long, 4–6 mm wide; carpels 5; styles absent, stigmas thinly coriaceous, suborbicular, peltate, 1.5–2 mm long and wide, thickening with age, flat in early ontogeny, convex at maturity; ovules numerous. Fruit yellowish-cream, suffused with purple along the carpel sutures, oblongoid, 2–3.5 cm long, 1.5–2.5 cm diam.

Common name.—“Jubaga bakoko” (Mui language, Colombia)

Distribution.—From lowlands of central Panama southward along the Pacific coast of Colombia (Chocó Floristic Province), along and below the western slopes of the Andean Cordillera Occidental of Ecuador, eastward through the Amazon Basin of Colombia and Brazil, and south-southwestward through the Amazon Basin of Ecuador, Peru and Bolivia, 100–400 (–1,690) m elevation.

Ecology and conservation status.—*Clusia amazonica* is a riparian species, tolerant of moderate amounts of disturbance but not capable of surviving long periods of inundation. It usually occurs high enough up in the canopy to permit some of the foliage to remain above periodic floodwaters. It occurs in várzea, igapó, tahuampa and other periodically inundated habitats. Unlike *Clusia martiana*, *C. amazonica* spends its entire life as a liana, and does not form large mats over the canopies of the trees. It is only very locally common, but is not considered threatened.

Specimens examined. COLOMBIA. Amazonas: Río Caquetá River Basin, 00°50'S, 71°50'W, 20 Nov 1991 (ster.), *J. Duivenvoorden et al.* 1259 (BRIT, COAH, COL, U); Mpio. Leticia, 03°47'S, 70°15'W, 100 m, 14 Apr 1991 (fr), *J. Pipoly* 15398 (BRIT, COL, FMB, MO); Antioquia: Mpio. San Francisco, Corregimiento Aquitania, Finca La Ilusión, 1,200–1,500 m, 2 Apr 1992 (stam. fl; pist. fr- mixed coll.), *R. Fonnegra et al.* 4129 (BRIT, COL, HUA, JAUM, MO). VENEZUELA. Amazonas: Depto. Atabapo, along Río Cunucunuma, near Culebra, 03°44'N, 65°44'W, 210 m, 15–16 Feb 1985 (stam. fl), *R. Liesner* 17516 (MO, VEN), (fr), *R. Liesner* 17535 (BRIT, MO, VEN); Salto Yureba, Caño Yureba, Bajo Ventuari, 04°03'N, 66°01'W, 120–150 m, 4 Nov 1981 (stam. fl bud), *F. Delascio & F. Guánchez* 10841 (MO, NY, US, VEN), 350 m, 15–16 Mar 1985 (pist. fl, fr), *R. Liesner* 18755 (MO, VEN); Depto. Atures, near Remo Camp, 04°34'N, 67°18'W, 180 m, Jun 1989 (fr), *E. Foldats & J. Velazco* 9580 (MO, PORT, VEN); Depto. Casiquiare, 12 km SE of San Fernando de Atabapo, Sector "El Pozo," CVG Experiment Station, 03°50'N, 67°47'W, 110 m, 10–16 Feb 1988 (pist. fl), *G. Aymard et al.* 6391 (MO, PORT, VEN); *G. Aymard et al.* 6404 (MO, PORT, VEN); Depto. Río Negro, Cerro de la Neblina, vicinity of base camp along Río Mawarinuma, affluent of Río Baria, 00°50'N, 66°10'W, 110–130 m, 8–10 Jan 1984 (stam. fl bud), *J. Steyermark & J. Luteyn* 129759 (F, MO, NY, US, VEN); Margins of Río Gavilán, between Raudal Gavilancito and Cerro Pelón, 05°37'N, 67°22'W, 80–120 m, 10–11 Feb 1992 (pist. fl), *G. Romero et al.* 2373 (AMES, MO, VEN). ECUADOR. Esmeraldas: Ecological Reserve Cotocachi-Cayapas, Parroquia Luís Vargas Torres, Río Santiago, Pote Salt Marsh, 00°49'N, 78°45'W, 250 m, 23–27 Oct 1993 (fr), *M. Tirado et al.* 539 (BRIT, QCNE, MO). Napo: Cantón Orellana, Parque Nacional Yasuní, "Maxus" road and oil pipeline, km 20, 00°33'S, 76°30'W, 250 m, 11–15 Aug 1993 (pist. fl bud), *M. Aulestia* 306 (BRIT, MO, QCNE); Conoco oil well "Amo II," 00°52'S, 76°05'W, 230 m, 29–30 Mar 1988 (fr), *F. Covello* 152 (BRIT, MO, QCNE); Cantón Tena, Jatun Sacha Biological Station, Río Napo, 8 km E of Misahualli, 01°04'S, 77°36'W, 450 m, 20 Jan 1990 (fr), *C. Cerón* 8386 (BRIT, MO, QCNE), 22–24 Feb 1988 (fr), *W. Palacios* 2489 (BRIT, MO, QCNE), 400 m, 17–28 May 1989 (fr), *W. Palacios* 4224 (BRIT, MO, QCNE), 17–28 May 1989 (fr), *W. Palacios* 4307 (BRIT, MO, QCNE), 6 May 1990 (fr), *W. Palacios et al.* 4954 (BRIT, MO, QCNE), 13 May 1990 (fr), *W. Palacios & E. Freire* 5105 (BRIT, MO, QCNE). 14 May 1990 (fr), *W. Palacios & E. Freire* 5145 (BRIT, MO, QCNE), Permanent Inventory along Río Chiguipino, 450 m, 22 May 1992 (fr), *E. Guidiño & J. Zuleta* 1660 (BRIT, MO, QCNE). Pastaza: Cantón Pastaza, "Masaramu" oil well, of UNOCAL, 40 km NNW of Montalvo, 00°44'S, 76°52'W, 400 m, 1–16 May 1990 (fr), *E. Guidiño* 362 (BRIT, MO, QCNE); PetroCanada road, Via Auca, 115 km S of Coca, 5 km S of Río Tigüino, 01°15'S, 76°55'W, 320 m, 26–31 Jan 1989 (fr), *D. Neill & F. Hurtado* 8749 (BRIT, MO, QCNE), 1–6 Mar 1989 (ster.), *V. Zak* 4119 (BRIT, MO, QCNE). Sucumbios: Cantón Gonzalo Pizarro, Campo Bermejo No. 6 Norte, 30 km NE of Lago Agrio, 00°14'N, 77°13'W, 1,050 m, 23 Mar 1990 (fr), *C. Cerón* 9227 (BRIT, MO, QCNE). PERU. Loreto: Prov. Maynas; Allpahuayo, Institute of Amazonian Investigations (IIAP) Experimental

Station, 04°10'S, 73°30'W, 150–180 m, Permanent Inventory, Plot A, Subplot 10, Nov 1991 (stam. fl), R. Vásquez & N. Jaramillo 14830 (AMAZ, BRIT, MO, USM), 27 May 1991 (ster.), R. Vásquez & N. Jaramillo 16618 (AMAZ, BRIT, MO, USM); Dtto. Fernando Lores, Caserío Serafín, Quebrada Tamshiyacu, from Caserío Serafín to Caserío Constancia, 125–130 m, 10 May 1991 (fr), C. Grández et al. 2606 (AMAZ, BRIT, MO, USM); Dtto. Iquitos, 1977 (stam. fl), J. Revilla 3312 (AMAZ, BRIT, F, MO, USM); Casería Mishana, Río Nanay, right bank, 20 Dec 1976 (stam. fl), J. Revilla 89 (AMAZ, F, MO, USM); Río Yarapa, 04°20'S, 73°30'W, 122 m, 20 Nov 1989 (stam. fl bud), C. Grández & J. Tapullima 1466 (AMAZ, MO, USM). **BOLIVIA.** Beni: Prov. Ballivian, Carinavi-San Borja Hwy, E side of Serranía del Pilón Lajas, 15°13'S, 67°03'W, 850 m, 2 Nov 1989 (fr), D. Smith & V. García 13865 (LPB, MO). La Paz: Prov. Nor Yungas, near Yolosa, at entrance to road to Chairo, 2 km from Chairo, 2,430 m, 5 Sep 1987 (pist. fl), S. Beck 12969 (LPB, MO); Prov. Morillo, Valle de Zongo, along trail from end of road at the Cahua Power Plant, 1,660–1,690 m, 23 Nov 1980 (pist. fl), T. Croat 51413 (LPB, MO), 16°05'S, 68°03'W, 1,400–1,600 m, 22 Apr 1982 (fr), J. Solomon 7491 (LPB, MO). **BRAZIL.** Amazonas: Alto Rio Solimões, Mpio. de São Paulo de Olivença, plateau S of city, road to Bom Fim, 25 Nov 1986 (stam. fl), C. Cid et al. 8552-A (BRIT, IAN, INPA, MG, NY). Pará: Ilha do Marajó, Rio Mocões, 2 km upriver from Anajás, 00°57'S, 49°56'W, 13 Nov 1987 (fr), S. Beck et al. 484 (BRIT, INPA, MG, NY), center of Iha Marajó, 27 Oct 1984 (stam. fl), G. Sobel et al. 4829 (BRIT, INPA, MG, NY). Rondônia: 28 km from Vilhena on road to Colorado, 13°00'S, 60°00'W, 29 Oct 1979 (fr), B. Nelson et al. 330 (BRIT, IAN, INPA, MG, NY).

Clusia amazonica is most closely related to *C. araracuarae*, but is readily distinguished by its smooth, obovate to elliptic leaf blades, muticous anthers, and inconspicuous latex canals. This species is apparently sympatric with *C. martiana*, but occurs in riparian forests above and away from the inundation zone. Forest inventory data indicate that *C. amazonica* is much more infrequent than *C. martiana*, and does not form large mats as the latter species does.

The type of *C. oedematopoidea* represents populations with smaller, less coriaceous leaves and smaller, more compact inflorescences than the Amazonian populations of *C. amazonica*. A collection from Antioquia, Colombia (R. Fonsegra et al. 4129) is identical to the type of *C. oedematopoidea*. Collections from Bolivia (S. Beck 12969, T. Croat 51413, J. Solomon 7491) resemble *C. martiana* in quantitative features of the leaves, but the prominent secondary veins and submarginal collecting vein, and, absence of significant numbers of latex canals visible on the adaxial leaf surface, clearly indicate they belong to *C. amazonica*.

3. *Clusia martiana* Engler, Fl. Bras. 12(1):411. 1888. (Fig. 3). TYPE: BRAZIL. AMAZONAS: Alto Amazonas, in forests of the Rio Japurá, Dec 1852 (stam. fl), C. Martius 3033 (HOLOTYPE: M, n.v.).

Clusia uleana Engler, Bot. Jahrb. 58:Beibl. 130:1. 1923. Syn. Nov. TYPE: BRAZIL. AMAZONAS: near Fortaleza, along Rio Juruá, 6 Nov 1901 (pist. fl bud), E. Ule 6006 (HOLOTYPE: B-destroyed, F Neg. 9205 !). A search for remaining duplicates of the type collection is underway and neo- or lectotypification is postponed until the whereabouts of duplicate collections is known, or if any are extant.

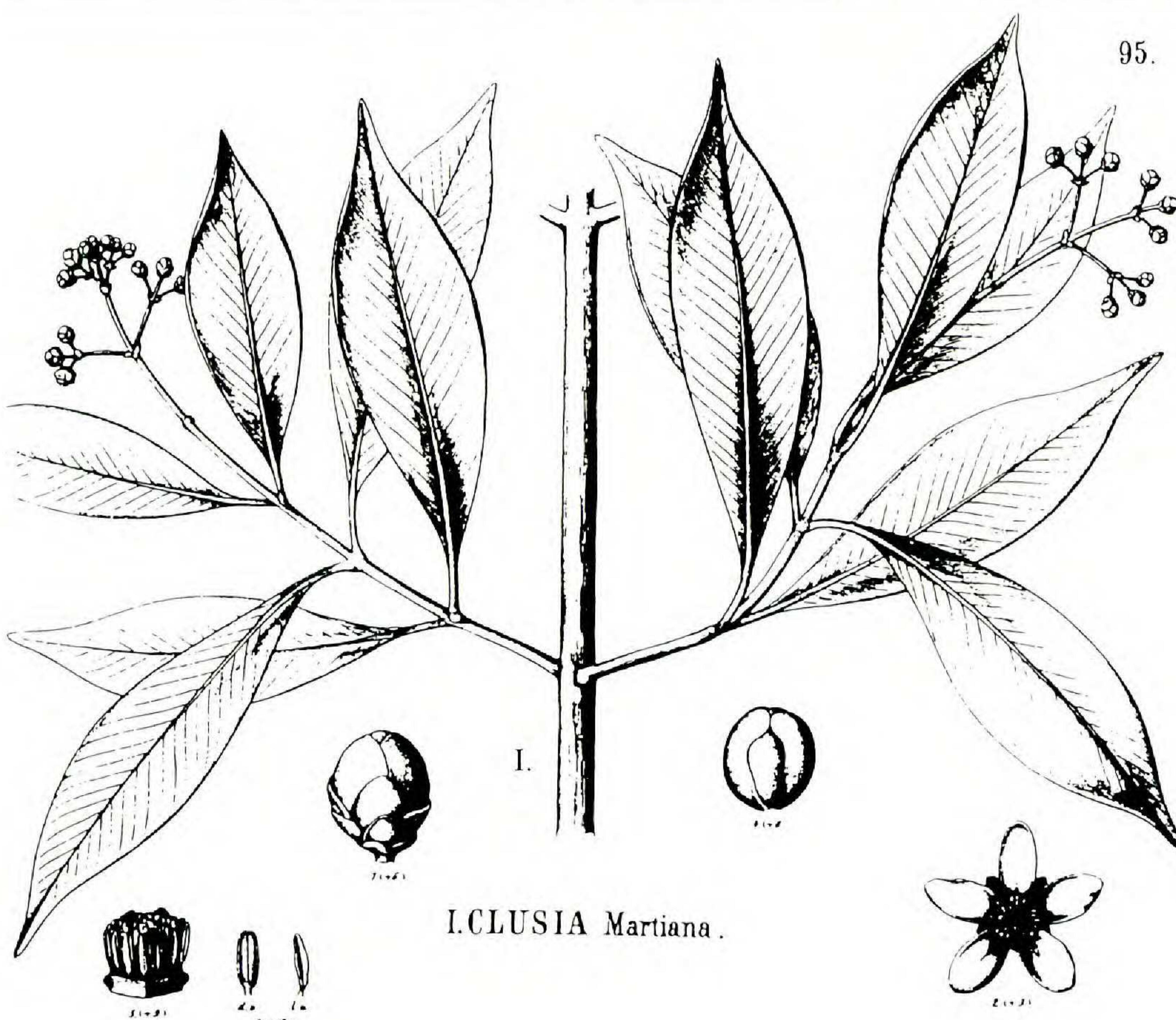


FIG. 3. *Clusia martiana* Engler. Habit (center); androecium, anthers in abaxial and lateral views, staminate flower bud, staminate flower bud with sepals and bracteoles removed, top view of staminate flower in anthesis (from left to right). Adapted from Engler in Martius, *Flora Brasiliensis*, 12:Plate 95.

Scendent epiphytic shrub, at times appearing lianous to 4 m tall; branchlets terete to somewhat tetragonal or pentagonal in cross section, at times squarrose, 2.5–3.5 mm diam., bark of apical portions rufous, scaly, checking transversely and exfoliate, rufous and glabrous at maturity, latex clear, moderate. Leaves decussate; blades subcoriaceous, obovate to oblanceolate, (6.5–)10–14.5 (–19) cm long, (2.3–)3.5–5.0(–6.5) cm wide, apex narrowly acute to abruptly acuminate, the acumen 0.3–1.5 cm long, base acute to cuneate, not decurrent on the petiole, smooth, glabrous above and below, sordid above, pallid below, latex canals dense and conspicuous above and below, midrib slightly raised above, prominently raised below, secondary veins numerous, smooth, inconspicuous above, slightly raised below, submarginal collecting vein barely discernible, the margin flat, entire, glabrous; petioles canaliculate, 1–1.5(–2) cm long, glabrous. Inflorescence terminal, pendent, pyramidal panicle, 2–4 cm long, 3–5 cm wide at

maturity, the flowers 3 per cyme; peduncle 0.8–1.5 cm long, subtended by normal leaves; secondary bracts coriaceous, oblate, 2.3–2.6 mm long, 3.5–4 mm wide, apex widely rounded, carinate, the margin somewhat hyaline, very narrowly scarious, entire, glabrous. Staminate inflorescence with tetragonal pedicels, the lateral 1.8–2.2, the terminal 2.5–3.5 mm long, glabrous; bracteoles 4, the outer 2 coriaceous, oblate, 2.3–2.6 mm long, 3.5–4 mm wide, apex widely rounded, carinate, the margin somewhat hyaline, very narrowly scarious, entire, glabrous, the inner 2 stiffly coriaceous, oblate, 2.5–3 mm long, 3.3–4.5 mm wide, apex broadly rounded, somewhat carinate, the margins entire, somewhat translucent, not scarious, glabrous. Staminate flowers white to yellow; sepals 5, contorted, membranaceous, very widely ovate, 5–7 mm long, 4–6 mm wide, apex broadly rounded, somewhat cucullate, densely lineate, the margin hyaline, scarious, glabrous; petals 5, contorted, carnose, oblong, 5.3–5.8 mm long, 1.8–2.2 mm wide, apex rounded, flat, obscurely lineate, the margin entire, opaque, not scarious, glabrous; androphore flat, pentagonal, the stamens numerous, free, 2.1–3.3 mm long at maturity, the filaments short, flat, anther 1–1.3 mm long, apex muticous, base truncate, dehiscent by longitudinal slits, the connective flat, truncate, darkened; pistillode absent. Pistillate flowers white, as in staminate but sepals orbicular, 3.5–4 mm long and wide; petals 4.5–5 mm long, 2.8–3.3 mm wide, apex obtuse to rounded; staminodes 5, 3–3.5 mm long, the filaments wide, 1 mm long, 2 mm wide, abruptly constricted apically to anthers, the anthers linear, ca. 1 mm long, 0.5 mm wide, apex muticous, base not distinguishable, with longitudinal slits, devoid of pollen, the connective darkened; pistil 4 mm long, 5 mm diam.; carpels 5; styles absent, stigmas thinly coriaceous, oblongoid, peltate, 1.8–2.2 mm long, 1–1.2 mm wide, flat in early ontogeny, convex at maturity; ovules numerous. Fruit greenish white with red hue in intercarpelary areas, ovoid, 2–3.5 cm long, 1.5–2.5 cm wide,

Distribution.—Amazon Basin of Colombia, Venezuela, Peru, Bolivia and Brazil, 100–450(–1,850) m elevation.

Ecology and conservation status.—*Clusia martiana* is a hemiepiphyte, growing along riverbanks, where it forms mats in and over the canopies of low trees, eventually killing them. This species can withstand extended periods submerged. I have seen the fruits floating on rivers, but it is doubtful that dispersion by fish is significant, because of the large numbers of small birds I have seen feeding from open capsules, on the red arillate seeds. It is commonly found on the margins of várzea, and “tahuampa” forests, which are on lateritic soils, but is also rarely found in sandy loams (“varillal”) and very rarely found in riparian forests with some pockets of white sand. *Clusia martiana* is one of the few weedy species of *Clusia*.

Specimens examined: COLOMBIA. Amazonas: Mpio. Leticia, Parque Nacional Natural Amacayacu, Matamatá trail, $03^{\circ}47'S$, $70^{\circ}15'W$, 110–120 m, 28 Oct 1991 (ster.), J. Pipoly 15610 (BRIT, COL, FMB, MO), near Quebrada Matamatá, 100 m, 11 Mar 1991 (fr), A. Rudas et al. 1542 (BRIT, COL, FMB, MO), along Quebrada Baccaba, 100 m, 16 Apr 1992 (fr), A. Rudas & A. Prieto 4286 (BRIT, COL, FMB, MO), along bank of Río Amacayacu, 100 m, 9 Apr 1991 (ster.), J. Pipoly et al. 15133 (BRIT, COL, FMB, MO); Vereda Puerto Nariño, $03^{\circ}45'S$, $70^{\circ}15'W$, 100 m, 3 Aug 1989 (ster.), R. Vásquez et al. 12510 (AMAZ, BRIT, COL, FMB, MO, USM). Antioquia: Mpio. Amalfí, 8–27 km NE of Almalfí, en route from Vetilla to Fraguas, near Salazar and Marengo, $06^{\circ}00'N$, $75^{\circ}04'W$, 1,150–1,450 m, 7 Dec 1989 (pist. fl), R. Callejas et al. 9114 (BRIT, COL, HUA); Mpio. Campamento, Vereda Llanadas, 6–12 km W of Campamento en route to Mina Las Brisas, $07^{\circ}05'N$, $75^{\circ}20'W$, 1,650–1,810 m, 7 Sep 1989 (pist. fl), R. Callejas et al. 8266 (BRIT, COL, HUA). VENEZUELA. Amazonas: Isla Sebastián, Río Casiquiare above Chapezón, between Boca and Solano, $01^{\circ}58'N$, $67^{\circ}03'W$, 120 m, 31 Jan 1980 (pist. fl), R. Liesner & H. Clark 8941 (MO, VEN); Depto. Atabapo, "Caño Iguapo, Alto Orinoco, 15 km SE of La Esmeralda, $03^{\circ}00'N$, $65^{\circ}28'W$, 150 m, 24 Feb 1990 (stam. fl), G. Aymard & L. Delgado 8227 (BRIT, PORT, VEN); Depto. Atures, Río Jénita floodplain, 7 km before Ocamo river mouth, $02^{\circ}46'N$, $64^{\circ}54'W$, 170 m, Feb 1990 (stam. fl), A. Fernández 7318 (BRIT, PORT, VEN); Río Mayaca, $02^{\circ}01'N$, $65^{\circ}07'W$, 228 m, 6 Feb 1989 (stam. fl), A. Henderson et al. 987 (BRIT, NY, VEN); Alto Orinoco, along riverside 2 hours above La Esmeralda, 26 Mar 1953 (stam. fl), B. Magnire & J. Wurdack 34708 (MO, NY, VEN); Río Padamo, 10 km above mouth, 27 Mar 1953 (stam. fl), B. Magnire & J. Wurdack 34718 (MO, NY, VEN); Depto. Casiquiare, near Capihuara, along Río Casiquiare, 5 Feb 1991 (pist. fl, fr), M. Collera et al. 1829 (BRIT, NY, VEN); Isla Sebastián, along Río Casiquiare between Boca and Solano, $01^{\circ}58'N$, $67^{\circ}03'W$, 120 m, 31 Jan 1980 (pist. fl), R. Liesner & H. Clark 8941 (MO, VEN). PERU. Cuzco: Dtto. Camantí, 8 km W of Quincemil, right margin of Río Manirí, toward the mouth of Río Araza, $13^{\circ}17'S$, $70^{\circ}48'W$, 720 m, 17 Jul 1990 (stam. fl), M. Timaná & H. Astete 646 (BRIT, CUZ, MO, USM). Junín: Mazamari, 1,000 m, 13 Sep 1960 (pist. fl, fr), F. Woytkowski 6019 (MO, US, USM). Loreto: Prov. Maynas, Buena Vista, Río Tahuayo, $04^{\circ}15'S$, $73^{\circ}10'W$, 140 m, 24 Jan 1981 (stam. fl), R. Vásquez & N. Jaramillo 1229 (AMAZ, F, MO, USM); Explornapo Camp, Quebrada Sucusari, Río Napo, $03^{\circ}15'S$, $72^{\circ}55'W$, 130 m, 30 May 1991 (ster.), A. Gentry et al. 74277 (AMAZ, BRIT, MO, USM), Explornapo Camp, $03^{\circ}20'S$, $72^{\circ}55'W$, 140 m, 18 Apr 1991 (fr), R. Vásquez & N. Jaramillo 16141 (AMAZ, BRIT, MO, USM); Vicinity of Iquitos, 1977 (stam. fl), J. Revilla 3254 (AMAZ, BRIT, F, MO, USM); Río Mamón, 6 Sep 1972 (stam. fl), T. Croat 20028 (AMAZ, MO, USM); Santa María de Nanay, 10 km W of Casería Mishana, Reserva Cocha Yaramá, along Río Nanay, $03^{\circ}55'S$, $73^{\circ}35'W$, 130 m, 15 Mar 1991 (ster.), J. Pipoly et al. 15031 (AMAZ, BRIT, MO, USM), (fr), J. Pipoly et al. 15036 (AMAZ, BRIT, CUZ, MO, USM); Río Itaya, below San Juan de Muniches, ca. 40 min above Iquitos, 120 m, 19 Mar 1977 (fr), A. Gentry et al. 18422 (AMAZ, F, MO, USM); Río Nanay, 6 turns above Iquitos, 28 Dec 1976 (pist. fl, fr), J. Revilla 2098 (AMAZ, F, MO, TEX, USM); Río Nanay between Iquitos and Puerto Almendras, 13 Jul 1976 (stam. fl), A. Gentry & J. Revilla 16710 (AMAZ, F, MO, USM); Dtto. Iquitos, Río Nanay, near Santa Clara, 19 Aug 1976 (stam. fl), J. Revilla 1144 (AMAZ, F, MO, USM), 13 Nov 1976 (stam. fl), J. Revilla 1899 (AMAZ, CUZ, F, HUT, MO, USM), 14 Nov 1976 (pist. fl bud), J. Revilla 1817 (AMAZ, F, MO, USM); Río Nanay, near Santa Clara, ca. 10 km above Morona Cocha, 150 m, 12 Dec 1976 (stam. fl), C. Davidson & J. Revilla 5415 (AMAZ, F, MO, USM); Nauta, Quebrada Saragosa, $04^{\circ}29'S$, $73^{\circ}35'W$, 200 m, 29 Mar 1987 (fr), R. Vásquez & N. Arévalo 9048 (AMAZ, MO,

USM); Río Yavarí, across river from Brazilian village of Pão Mari, 23 Nov 1977 (stam. fl), A. Gentry & J. Revilla 20814 (AMAZ, BRIT, CUZ, F, HUT, MO, TEX, USM); Along Río Blanco, above Tamshiyacu, 140 m, 17 Mar 1978 (fr), C. Díaz et al. 215 (AMAZ, CUZ, F, MO, USM); Caserío Nina Rumi, along Río Nanay, 23 Feb 1976 (fr), J. Revilla 199 (AMAZ, MO, USM); San Antonio, Río Pintuyacu, $03^{\circ}40' S$, $73^{\circ}54' W$, 160 m, 21 Apr 1986 (fr), R. Vásquez et al. 7487 (AMAZ, CUZ, F, MO, USM); Quebrada Yanayacu, tributary of Río Manatí, $03^{\circ}45' S$, $72^{\circ}55' W$, 110 m, 25 Jan 1989 (pist. fl, fr), R. Vásquez & N. Jaramillo 11573 (AMAZ, BRIT, MO, US). **BOLIVIA.** La Paz: Río Saturiapo, 14 km SW of Ixiamas, second ridgeline, $13^{\circ}53' S$, $68^{\circ}15' W$, 620–650 m, 2 Jun 1990 (bud), A. Gentry & R. Foster 70864 (F, LPB, MO); Prov. Nor Yungas, 4.5 km below Yolosa, then 14 km W on road along Río Huarinilla, on abandoned road to Hacienda Sandillan, S side of river, $16^{\circ}12' S$, $67^{\circ}50' W$, 1,200–1,300 m, 24 Jan 1983 (fr), J. Solomon 9391 (LPB, MO); Prov. Murillo, 1/2–3/4 by trail downriver from the Cahua Hydropower Plant, $16^{\circ}05' S$, $68^{\circ}03' W$, 1,400–1,600 m, 22 Apr 1982 (fr), J. Solomon 7491 (LPB, MO); 44 km below Lago Zongo Dam, vicinity of Cahua hydroelectric plant, $16^{\circ}03' S$, $68^{\circ}01' W$, 1,200 m, 12–15 Sep 1983 (stam. fl), J. Solomon 10829 (LPB, MO). **BRAZIL.** Roraima: SEMA Ecological Reserve, Ilha de Maracá, Parimiu, $03^{\circ}20' N$, $62^{\circ}58' W$, 24 May 1987 (fr), W. Milliken & S. Bowles 276 (MO).

Clusia martiana is isolated within the section, but may be more closely related to *C. amazonica* than to *C. araracuarae*. It is readily separated from both of those species by the subcoriaceous leaves with acute to cuneate bases, the highly conspicuous, numerous linear latex canals, and barely discernible submarginal collecting vein. I have observed that *C. martiana* is an epiphytic shrub at first, then becomes lianous with age. *Clusia martiana* is most frequently confused with *C. (section Brachystemon) penduliflora* because they share the nearly the same habit, have relatively short inflorescences (compared to *C. amazonica*), and are partially sympatric. However, the oblongoid stigmas, flattened, longer filaments and subcoriaceous leaves of *C. martiana* easily distinguish it from *C. penduliflora* and *C. amazonica*.

The type of *Clusia uleana* represents those populations of *C. martiana* with short branches and inflorescences, and slightly larger flowers than those of the average population. However, it is otherwise identical to the majority of *C. martiana* populations. The type specimen was destroyed in Berlin, and no duplicate has been found in HBG or other herbaria thus far. However, the Field Museum of Natural History (F) photograph clearly shows the characteristic squarrose branchlet tips with horizontally checking and exfoliating bark, numerous, very highly conspicuous foliar linear latex canals, and obscure secondary venation, thus confirming its identity as *Clusia martiana*.

Clusia section Brachystemon (Engler) Pipoly, comb. nov. *Clusia* section *Criuva* subsection *Brachystemon* Engler in Martius, Fl. Bras. 12(1):412. 1888. LECTOTYPE SPECIES (here designated): *Clusia spathulaefolia* Engler in Martius, Fl. Bras. 12(1):412. 1888.

Clusia section *Criuva* subsection *Criuvopsis*, pro parte, Vesque, Monogr. Phan. 8:34. 1893.
Clusia subgenus *Criuva* Bentham section *Brachystemon* (Engler) Engler, Pflanzenfam. 3(6):225. 1893.

Free-standing trees or hemiepiphytes; latex white or cream. Leaves petiolate. Inflorescence a terminal panicle; branches cymose; secondary inflorescence bracts 2, carnose; bracteoles 4, decussate, carnose or coriaceous. Perianth erect, sepals 5–9, membranaceous or coriaceous, the outer 2 opposite, the others contorted; petals 4–5, contorted, chartaceous, coriaceous or thickly carnose; androphore pentagonal; stamens numerous, subsessile on free, short, terete or prismatic filaments; anthers linear, basifixed, muticous, much longer than the filaments, apically truncate or emarginate, dehiscent by longitudinal slits; pistillode absent or very reduced, the central receptacle resiniferous. Pistillate inflorescence and flowers as in stamine, but staminodia 5, free, the filament broad, abruptly tapering apically, anther linear, apex muticous; carpels 5; ovules horizontal; stigmas sessile, peltate, elliptic or narrowly triangular. Fruit a capsule, oblongoid or depressed-globose, stigmas persistent.

Distribution.—Three species in the Amazon Basin and adjacent Andes of Colombia, Venezuela, Ecuador, Peru, Bolivia and Brazil.

Clusia section *Brachystemon* is most closely related to section *Criuvopsis*, but is separated by the short, subterete or prismatic filaments of the anthers, and compact inflorescences with relatively thicker rachises. It is restricted to the Amazon Basin and adjacent Andes of South America, often along riverbanks. The three species of the section can be separated by the following key.

KEY TO SPECIES OF *CLUSIA* SECTION *BRACHYSTEMON*

1. Hemiepiphytes; leaf blade coriaceous, dull above and below, the apex broadly rounded to an abruptly acuminate tip; flowers on pedicels 3–10 mm long; stigmas elliptic; fruits smooth, not ribbed 1. *C. penduliflora*
1. Free-standing trees; leaf blade stiffly coriaceous to cartilaginous, nitid above, pallid below, the apex broadly rounded to truncate, without acuminate tip; flowers sessile to subsessile, the pedicels less than 1 mm long; stigmas cuneiform; fruits strongly ribbed.
 2. Leaf blades oblanceolate to obovate, the base attenuate, decurrent on the petiole, the margins revolute; petioles broadly marginate, 1–1.5(–2.2) cm long; branchlets 7–10 mm diam. 2. *C. spathulaefolia*
 2. Leaf blades oblong to elliptic, the base obtuse to broadly rounded, not decurrent on the petiole, the margins flat; petioles subterete, 3–4.5(–5) cm long; branchlets 10–22 mm diam. 3. *C. aymardii*
1. ***Clusia penduliflora* Engler, Fl. Bras. 12(1):412. 1888. (Fig. 4). TYPE.**
 BRAZIL. AMAZONAS: Near Panure along Rio Uaupes, Dec 1852 (stam. fl), R. Spruce 2792 (HOLOTYPE: G, n.v.; ISOTYPE: P!).

Hemiepiphyte; branchlets quadrate to subterete, 3.5–5 mm diam., gla-

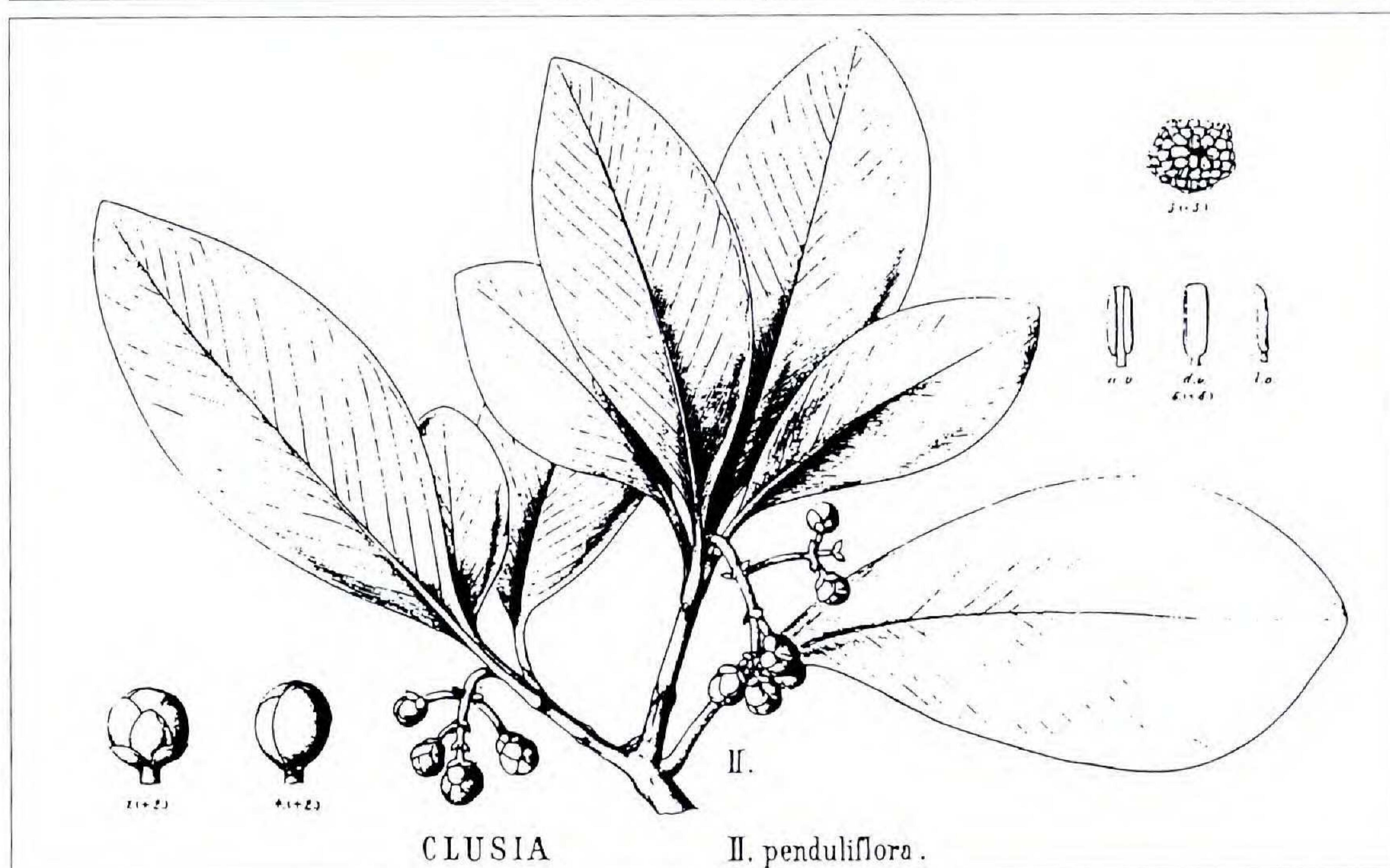


FIG. 4. *Clusia penduliflora* Engler. Habit (center); staminate flower bud, staminate flower bud with sepals and bracteoles removed (lower left, from left to right); top view of androecium (upper right); anthers in adaxial, abaxial and lateral views (right side, left to right). Adapted from Engler in Martius, *Flora Brasiliensis* 12:Plate 84.

brous, bark gray to grayish-brown, not transversely checked or exfoliating; glabrous; latex white to cream, scanty. Leaves decussate; leaf blades coriaceous, obovate to rarely elliptic, (8.8–)14–22.5 cm long, (3–)6.5–11.0 cm wide, apex broadly rounded to an abruptly acuminate tip, or rarely acute, base obtuse to acute, not decurrent on the petiole, dull above and below, at times with numerous, conspicuous latex canals, midrib raised above, prominently raised below, secondary veins inconspicuous, numerous, extending to the margin, without submarginal collecting vein, the margin flat, entire, glabrous; petioles canaliculate, 1.3–1.7(–2.3) cm long, glabrous. Inflorescence: terminal, pendent, pyramidal paniculate, 3–7(–8.5) cm long, 3–8 cm wide, the branches cymose, 3-flowered at inflorescence apex, 2–3 flowers per cyme below; peduncle (0.7–)1–2 cm long, subtended by normal leaves; secondary bracts carnose, depressed ovate, 2–3 cm long, 2.5–3.5 cm wide, apex rounded, carinate, the margin opaque, not scariosus, entire, glabrous. Staminate inflorescence with tetragonal pedicels, 3–10 mm long, glabrous; bracteoles 4, decussate, carnose, the outer 2 suborbicular, 3–4 mm long, 3–3.5 mm wide, apex broadly rounded, medially carinate, the margins entire, opaque, not scariosus, the inner 2 coriaceous, orbicular, 5–6 mm long and wide, apex broadly rounded, carinate, the margin entire, opaque, scariosus. Staminate flowers greenish pink; sepals 7–9, the outer se-

pals 2, opposite, coriaceous, suborbicular to oblate, 5–6 mm long, 6–7 mm wide, apex very widely rounded, subcucullate, the margin entire, scarious, the inner sepals 5–7, contorted, membranaceous, brittle, very widely ovate, 6–7 mm long, 5–7 mm wide, translucent, apex rounded, venation prominent, the margin hyaline, scarious; petals 5, contorted, coriaceous, widely obovate, 5–7 mm long, 3–4 mm wide, apex truncate to very broadly rounded, linear latex canals numerous, prominent, the margin hyaline; androphore flat or slightly convex, the stamens numerous, free, 3.5–3.8 mm long, the filaments short, terete, ca. 1 mm long, the anthers linear, 2.5–3.5 mm long, ca. 0.5 mm wide, apex truncate, base truncate to broadly obtuse, dehiscent by longitudinal slits, the connective terete, darkened; pistillode subobsolete to obsolete, resiniferous. Pistillate inflorescence as in staminate but with outer bracteoles 2.5–3.5 mm long, 2.5–3.5 mm wide, inner 2 bracteoles suborbicular to oblate, 2–3.5 mm long, 2.5–4 mm wide pedicels subobsolete to 3 mm long. Pistillate flowers green, as in the staminate but sepals suborbicular, 3.5–5 mm long, 5–7 mm wide, the inner sepals suborbicular to very widely ovate, 5–8 mm long, 5–7 mm wide; petals prominently cucullate; staminodes 5, flat, 3.5–4 mm long, the filaments 2–2.5 mm long, 2–2.2 mm wide, abruptly tapering apically; anthers rectangular, 1–1.2 mm long, 0.5–0.6 mm wide, muticous apically, the connective darkened, the thecae not fully differentiated and devoid of pollen; pistil subglobose, 4–6 mm long and in diam.; carpels 5; styles absent; stigmas thinly coriaceous, elliptic, peltate, 1.5–2 mm long, 1–1.5 mm wide, persistent, flat in early ontogeny, convex at maturity; ovules numerous. Fruit green, oblongoid, 2–3.5 cm long, 1.3–2.5 cm diam.

Common names.—“Matapalo” (Napo-Ecuador).

Distribution.—Central and western Amazonia of Brazil, Colombia, Ecuador and Peru, 50–500(–1,800) m elevation. *Clusia penduliflora* is expected to occur in Amazonian Venezuela in forests on *terra firme*. Its apparent absence there is probably a collection artifact.

Ecology and conservation status.—*Clusia penduliflora* is a hemiepiphyte that grows in primary lowland moist, wet and rain forests, on alluvial terraces just above floodplains. It may be found in tree canopies in areas of high incident light near the transition zones with varzea forests.

Specimens examined. COLOMBIA. Chocó: Along Río San Juan, near Docordó, 0–100m, 04°15'N, 77°22'W, 29 Mar 1979 (stam. fl), E. Forero et al. 4328 (COL, MO); road to Cabí, SW of Tutunendo, 100 m, 19 Jan 1979 (pist. fl), A. Gentry & E. Rentería 24444 (COL, JAUM, MO). ECUADOR. Esmeraldas: Lita-San Lorenzo Road, ca. 30 km NW of Lita, 01°05'N, 78°40'W, 300–500 m, 12 May 1991 (fr), A. Gentry et al. 70025 (BRIT, MO, QCNE). Morona-Santiago: Campamento La Playa, road construction camp 23 km SE of San Juan Bosco, 1,050 m, 28 Jan 1981 (stam. fl), A. Gentry et al. 30932 (MO, SEL). Napo: Cantón Aguarico, Reserva Faunística Cuyabeno, Laguna Zancudo Cocha (Iripari), 00°33'S,

75°32'W, 230 m, 28 Sep 1991 (pist. fl), W. Palacios et al. 7770 (MO, QCNE); Cantón Tena; Jatun Sacha Biological Station, Río Napo, 8 km below Misahuallí, 01°04'S, 77°36'W, 450 m, 17 Jan–6 Feb 1987 (pist. fl), C. Cerón 614 (MO, QCNE), 17–28 May 1989 (fr), W. Palacios 4274 (BRIT, MO, QCNE), 14 May 1990 (fr), W. Palacios & E. Freire 5151 (MO, QCNE), 17–24 Feb 1988 (stam. fl), C. Cerón 3622 (MO, QCNE), 24 Nov 1987 (pist. fl), D. Neill & S. Manning 8013 (MO, QCNE); Parque Nacional Yasuní, "Daimi" Oil Well 2, 00°55'S, 76°11'W, 200 m, 26 May–8 Jun 1988 (fr), C. Cerón & F. Hurtado 4084 (MO, QCNE); Limnococha, NE of runway, Feb 1970 (stam. fl), R. Mowbray 7026 (MO, SEL). Pastaza: Via Auca, 110 km S of Coca, 10 km from Río Tigüino, sector Cristal, 01°15'S, 76°55'W, 320 m, 7 Jan 1989 (pist. fl), W. Palacios et al. 3433 (BRIT, MO, QCNE). Canton Pastaza, "Ramirez" Oil Well, 20 km S of Curaray, 01°32'S, 76°51'W, 300 m, 21–28 Feb 1990 (fr), V. Zak et al. 5292 (BRIT, MO, QCNE). Pichincha: Cooperativa Santa Marta No. 2, along Río Verde, 2 km SW of Sto. Domingo de Los Colorados, 530 m, 5 Feb 1979 (pist. fl), C. Dodson 7418 (MO, QCA, SEL). Sucumbios: Canton Gonzalo Pizarro, Campo Bermejo 6 N, 30 km NW of Lago Agrio, 00°14'N, 77°13'W, 1,050 m, 23 Mar 1990 (fr), C. Cerón et al. 9120 (BRIT, MO, QCNE); Parroquia Reventador, PreCooperativa Garcia Moreno, 3rd line N of road, near Río Due, 00°03'N, 77°35'W, 1,800 m, 23 May 1990 (fr), C. Cerón et al. 9841 (BRIT, MO, QCNE). PERU. Cuzco: Prov. Quispicanchis, Camantí, Manirí, along Río Manirí, trail to Quebrada Garrote, 13°71'S, 70°45'W, 720 m, 8 Sep 1990 (stam. fl), M. Timaná 924 (AMAZ, BRIT, CUZ, F, MO, USM); hills around Río Araza between Pan de Azucar and Quince Mil Airport, 292 km from Cusco, 13°13'S, 70°45'W, 643 m, 10 Aug 1991 (stam. bud), P. Nuñez 14081 (CUZ, HUT, MO, USM). Loreto: Prov. Maynas; forest behind Caseria Mishana, 150 m, 13 Nov 1977 (pist. fl), A. Gentry et al. 20673 (AMAZ, MO, USM); Río Gueppi, tributary of Río Putumayo, Peru/Ecuador border, 200 m, 14 May 1978 (fr), A. Gentry et al. 21842 (AMAZ, MO, USM); Dtto. Fernando Lores; Caserio Constancia (Quebrada Tamshiyacu), 04°08'S, 72°55'W, 120–130 m, 7 May 1991 (fr), C. Grández et al. 2472 (AMAZ, BRIT, MO, USM); Dtto. Pevas; Caserio Colonia (Quebrada Sumón), tributary of Río Yahuasyacu, trail to Río Putumayo, 03°20'S, 71°50'W, 120–130 m, 30 Mar 1991 (fr), Grández et al. 2334 (AMAZ, BRIT, MO, USM); San Antonio, Río Itaya, 04°10'S, 73°20'W, 13 Dec 1982 (stam. fl), R. Vásquez & N. Jaramillo 3558 (AMAZ, MO, USM); Prov. Requena, Jenaro Herrera, Río Ucayali, 04°55'S, 73°45'W, 22 Feb 1987 (fr), A. Gentry et al. 56361A (AMAZ, MO, USM); Sapuena, Bagazan-Río Ucayali, 04°45'S, 73°38'W, 130 m, 14 Jan 1987 (pist. fl), R. Vásquez & N. Jaramillo 8789 (AMAZ, MO, USM). BRAZIL. Amazonas: Dtto. Agropecuario, Reserva 1051 ("km 41") of the WWF/INPA MCS Project; 02°25'31"S, 59°45'50"W, 50–125 m, 20 Nov 1988 (stam. fl), B. Boom et al. 8568 (BRIT, INPA, NY), 02°24'26"- 02°25'31"S, 59°43'40"- 59°45'50"W, 6 Dec 1988 (pist. fl), B. Boom et al. 8764 (BRIT, INPA, NY), (stam. fl), S. Mori et al. 20194 (BRIT, INPA, NY); Municipality of São Paulo de Olivença, near Palmares, 11 Sep–26 Oct 1936 (stam. fl), B. A. Krukoff 8324 (MO, NY, US); Municipality Oriximiná, BR 163 to 7 km N of Cachoeira Porteira, near ES-7, 01°02'S, 57°02'W, 20 Aug 1986 (stam. fl), C. A. Cid et al. 7929 (BRIT, MG, INPA, NY).

Clusia penduliflora is most closely related to *C. spathulaefolia*, but is readily separated by its hemiepiphytic habit, leaves with long petioles, cuneate bases, obscure secondary venation and conspicuous latex canals, and the relatively small, pendent inflorescences. This species is often confused with *Clusia martiana*, but may be readily separated in flower by its subsessile anthers. Vegetatively, *Clusia penduliflora* generally has larger leaves and an

erect habit, but this character overlaps between the two species considerably. In fruit, *C. penduliflora* has an oblongoid fruit with elliptic stigmas, while *C. martiana* has ovoid fruits with oblongoid stigmas.

3. Clusia spathulaefolia Engler, Fl. Bras. 12(1):412. 1888. TYPE. BRAZIL.

AMAZONAS: Alto Amazonas, along streams near Panuré, along Rio Uaupes, Dec 1852 (stam. fl), R. Spruce 2782 (HOLOTYPE: B-destroyed, F Neg. 32279!; LECTOTYPE (here designated): P!).

Free-standing trees to 20 m tall, 35 cm DBH; branchlets 4-angled with narrow ridges approximately 2 mm tall, 7–10 mm diam., bark gray to grayish-brown, smooth, not transversely checked or exfoliating, glabrous; latex white, copious. Leaves decussate; leaf blades stiffly coriaceous to cartilaginous, oblanceolate to obovate, rarely elliptic, (12–)19–28 cm long, (3.5) 10(–16.8) cm wide, apex obtuse to broadly rounded, base attenuate and decurrent on the petiole, nitid above, dull below, latex canals inconspicuous, midrib raised but canaliculate above, prominently raised below, secondary veins numerous, raised above, slightly raised below, extending to a fine submarginal collecting vein, the margin revolute, entire, glabrous; petioles broadly marginate, 1–1.5(–2.2) cm long, glabrous. Inflorescence terminal, erect, pyramidal paniculate, 5–8(–10) cm long, 5–7(–10) cm wide, the branches cymose, the flowers solitary or 3 per cyme; peduncle 1–2.5(–5) cm long, subtended by normal leaves; secondary bracts carnose, widely ovate, 3–7 mm long, 4–6 mm wide, apex obtuse to rounded, carinate, the margin scariosus, entire, glabrous. Staminate inflorescence with tetragonal pedicels, within each cyme, the pedicels of the lateral flowers 0.6–1 mm long, those of the terminal flower 3–5 mm long, glabrous; bracteoles 4, the outer 2 carnose, widely ovate, 3–7 mm long, 4–6 mm wide, apex obtuse to rounded, carinate to crested medially, the margin scariosus, hyaline, entire, glabrous, the inner 2 coriaceous, orbicular to oblate, 4–4.5 mm long, 3–3.5 mm wide, apex broadly rounded, somewhat carinate, the margins scariosus, hyaline, entire, glabrous. Staminate flowers white; sepals 7(–8), the outer sepals 2, opposite, chartaceous, brittle, orbicular, 5–7 mm long and wide, apex broadly rounded, cucullate, the margin entire; the inner ones 5, contorted, membranaceous, brittle, very widely ovate, 4–6 mm long, 3–5 mm wide, largely opaque, apex very broadly rounded to subtruncate, translucent latex canals dense, cucullate, the margin hyaline, entire, scariosus; petals 5, thickly carnose, obovate-spathulate to oblong, 5–7 mm long, 2–2.5 mm wide, apex truncate, venation and latex canals prominent, medially thickened, the margin undulating, entire, translucent, glabrous; androphore flat or slightly concave, quadrangular, the stamens numerous, free, 2.5–3.3 mm long, the filaments prismatic, 0.5–0.8 mm long, the

anthers linear, 2–2.5 mm long, 0.5 mm wide, apex truncate, base truncate, dehiscent by longitudinal slits, the connective prismatic, darkened; pistillode obsolete. Pistillate inflorescence as in staminate but with pedicels 2–3 mm long; outer bracteoles suborbicular, 3–3.5 mm long, 3–4 mm wide, the inner 2 4–5.5 mm long, 5–6 mm wide. Pistillate flowers white, as in the staminate but sepals suborbicular, 5–7 mm long, 3.5–5 mm wide; petals obovate-spathulate, 5–7 mm long, 2.5–3 mm wide, apex rounded, abruptly constricted toward base; staminodes 20, to 2 mm long, the filament flat, 0.3–0.5 mm long, anther linear, 1.3–1.5 mm long, 0.3–0.5 mm wide, not bearing pollen; pistil subglobose, 5–8 mm long, and in diam., narrowing toward the apex; carpels 5; the ovules numerous, the styles absent; stigmas sessile, cuneiform, convex, 2–3.5 mm long, 1.5–2 mm wide. Fruit pale green, tinged with pink in intercarpelary grooves, depressed-globose, 1.5–1.8(–2) cm long, 2.2–2.5(–2.8) cm diam.

Common names.—COLOMBIA: “Matapalo” (Spanish); “Detziva” (Miraña language); “Atbo-caja-jubaga-bacoco-moho” (Mui language); “Jubagagaimio” (Mui language-elders); “Jipeo” (Hui language). VENEZUELA: “Cupí banero hoja gruesa,” “Cupí”.

Distribution.—Endemic to the Guayana Crystalline Shield of Venezuela, Brazil, and Colombia, with a disjunct population in Peru, at 50–200 (–1,650) m elevation.

Ecology and conservation status.—*Clusia spathulaefolia* is a medium-sized, free-standing tree growing in gallery scrub forests (“Bana”) and savannas (“campinarana” or “amazonian caatinga”) along black water rivers, on deep white sands. These formations are near rivers but do not flood (Macedo & Prance 1978; Prance 1979; Prance & Schubart 1978).

Specimens examined. COLOMBIA. Caquetá: Araracuara, N side of the central portion of the airstrip; 27 Apr 1988 (ster.), M. Sanchez et al. 131 (COAH, MO), Near the airport, 00°37'S, 72°24'W, 17 Oct 1990 (fl bud), J. Duivenvoorden & A. Cleef 258 (BRIT, COAH, COL, U), 15 Nov 1991 (ster.), J. Duivenvoorden 980 (BRIT, COAH, COL, U). Amazonas: Río Caquetá, right bank, 1.8 km above the mouth, Quinche, 2.7 km; 11 May 1988 (fr), M. Sanchez et al. 341 (COAH, MO); Río Caquetá, left bank, 1 km above the W end of Mariñame Island, 3.5 km; 13 Jun 1988 (fr), M. Sanchez et al. 744 (COAH, MO), Jun 1989 (ster.), L. Urrego 578 (COAH, MEDEL, MO), Jul 1989 (ster.), L. Urrego 721 (COAH, MEDEL, MO); Cuenca Río Caquetá, 00°50'S, 71°50'W, 22 Nov 1991 (stam. fl bud), J. Duivenvoorden et al. 1361 (BRIT, COAH, COL, U); Quebrada el Tigre, 8 km N of mouth, 2 km, 20 Sep 1988 (immature bud), M. Sanchez et al. 1347 (COAH, MO). Vaupés: Amazon Basin, Río Negro, San Felipe de Vaupés, 200 m, 13–25 Nov 1952 (ster.), H. Humbert 27511 (COL, P). VENEZUELA. Amazonas: Depto. Atabapo, SE bank of middle portion Caño Yagua at Cucurital de Yagua, 03°36'N, 66°34'W, 120 m, 8 May 1979 (pist. fl, fr), G. Davidse et al. 17404 (MO, US, VEN); below Salto Los Monos, on tributary of headwaters of Río Iguapo, 03°35'N, 65°23'W, 1500–1650 m, 12 Mar 1985 (fr), R. Liesner 18601 (MO, VEN); third slope, on Río Atacavi, 03°12'N, 67°24'W, 100 m, Nov 1989 (fr), J.

Velazco 1126 (BRIT, PORT, VEN); Depto. Atabapo/Casiquiare, El Almidón, Río Atacavi, slope 2, 03°04'N, 67°06'W, 80 m, Nov 1989 (stam. fl bud), *J. Velazco* 870 (BRIT, PORT, VEN). Depto. Atures, Second camp 110 km above Río Guayapo, 04°18'N, 67°28'W, 120 m, May 1989 (fr), *E. Foldats & J. Velazco* 9318 (BRIT, NY, MO, PORT); Depto. Casiquiare, Caño San Miguel, sector "Las Tinajas," 02°39'N, 66°45'W, 160 m, 25 Apr 1991 (fr), *G. Aymard* 9232 (BRIT, PORT, VEN); Depto. Río Negro, Bona, 10 km NE of San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro & Brazo Casiquiare, 01°56'N, 67°03'W, 119 m, 21 Dec 1978 (pist. fl), *H. Clark & P. Maquirino* 6907 (BRIT, MO, VEN), 6 May 1979 (pist. fl, fr), *H. Clark* 7172 (MO, VEN), 2 Mar 1979 (pist. fl, fr), *H. Clark* 7053 (MO, VEN), 7 Apr 1979 (pist. fl, fr), *R. Liesner* 6302 (MO, VEN), 16 Apr 1979 (pist. fl, fr), *R. Liesner* 6692 (MO, VEN), 25 Jan 1985 (stam. fl), *B. Boom et al.* 5361 (GH, NY, US, VEN); Alto Río Negro, Yapacana Savanna, 16 Mar 1953 (pist. fl), *B. Maguire & J. Wurdack* 34547 (MO, NY, US, VEN), (stam. fl), *B. Maguire & J. Wurdack* 34574 (F, MO, NY, US, VEN), *B. Maguire & J. Wurdack* 34575 (F, MO, NY, US, VEN); Sierra de Unturán, 01°33'N, 65°12'W, 1,150 m, 3 Feb 1989 (stam. fl), *A. Henderson* 941 (BRIT, NY, VEN); Cerro de la Neblina base camp, Río Mawarinuma, 00°50'N, 66°10'W, 140 m, 8 Feb 1995 (pist. fl), *B. Boom & A. Weitzman* 5698 (BRIT, F, GH, MO, NY, US, VEN). PERU. Loreto: Campamento Petrolero San Jacinto, Río Tigre, 02°15'S, 75°50'W, 200 m, 16 Sep 1979 (pist. fl, fr), *C. Díaz & N. Jaramillo* 1463 (AMAZ, F, MO, USM). BRAZIL. Amazonas: Município Pres. Figueiredo, Rio Uatumã, Igarapé Catitu, right margin, 01°- 02°S, 59°- 60°W, 29 Mar 1986 (fr), *C. Cid et al.* 7014 (BRIT, INPA, MG, NY); Km 130, Manaus-Caracaraí Rd., 1 Dec 1974 (stam. fl), *A. Gentry* 12960 (INPA, MO); Município São Gabriel do Cachoeira, Ilha Tamanduá, at mouth of Rio Uaupés (Rio Caiari), 2 km above Cumunidade Jowavira, near Ilha de Flores, 30 Dec 1989 (fr), *B. Nelson et al.* 1719 (BRIT, MG, INPA, NY); Rio Negro, near mouth of Rio Xié, opposite São Marcelino, 00°55'N, 67°15'W, 21 Oct 1987 (fr), *D. Stevenson et al.* 779 (BRIT, INPA, MG, NY). Pará: Município de Itaituba, Serra do Cachimbo, Base Aérea, 5 km behind the Cachimbo Airport, along bank of Rio Formiga, 27 Apr 1983 (fr), *M. N. Silva et al.* 136 (BRIT, INPA, MG, NY).

Clusia spathulaefolia is most closely related to *C. aymardii*, the two having free-standing, terrestrial habit, stiffly coriaceous to cartilaginous and nitid leaf blades with rounded to truncate apices, the subsessile to sessile flowers, cuneiform stigmas and strongly ribbed fruits in common. *Clusia spathulaefolia*, along with *Clusia pusilla* Steyermark, and several species of Myrsinaceae, most notably *Cybianthus spicatus* (H.B.K.) Agostini, and *C. fulvopulverulentus* (Mez) Agostini subsp. *magnoliifolius* (Mez) Pipoly, all grown on Serra do Cachimbo, suggesting that it may be a tepui satellite not previously listed in Maguire's (1979) treatise on the phytogeography of the Guayana Highland.

3. *Clusia aymardii* Pipoly, sp. nov. (Fig. 5)

Ob habitu arboreum, folia rigido-coriacea vel cartilaginea, supra nitida subter pallidaque, ad apicem late rotundata vel truncata, flores sessiles vel subsessiles, pedicelos usque 1 mm longos necnon stigmatibus cuneiformibus denique fructus praecclare costatus. *C. spathulaefoliae* valde arcte affinis, sed ab ea laminis oblongis vel ellipticis (nec oblanceolatis vel obovatis), ad basem obtusis vel late rotundatis (nec attenuatis), secus marginis planis (nec revolutis), petiolis subteretibus (non marginatis) 3–5 (nec 1.5–2.2) cm longis, et ramulis 10–22 (non 7–10) mm in diametris facile cognoscitur.

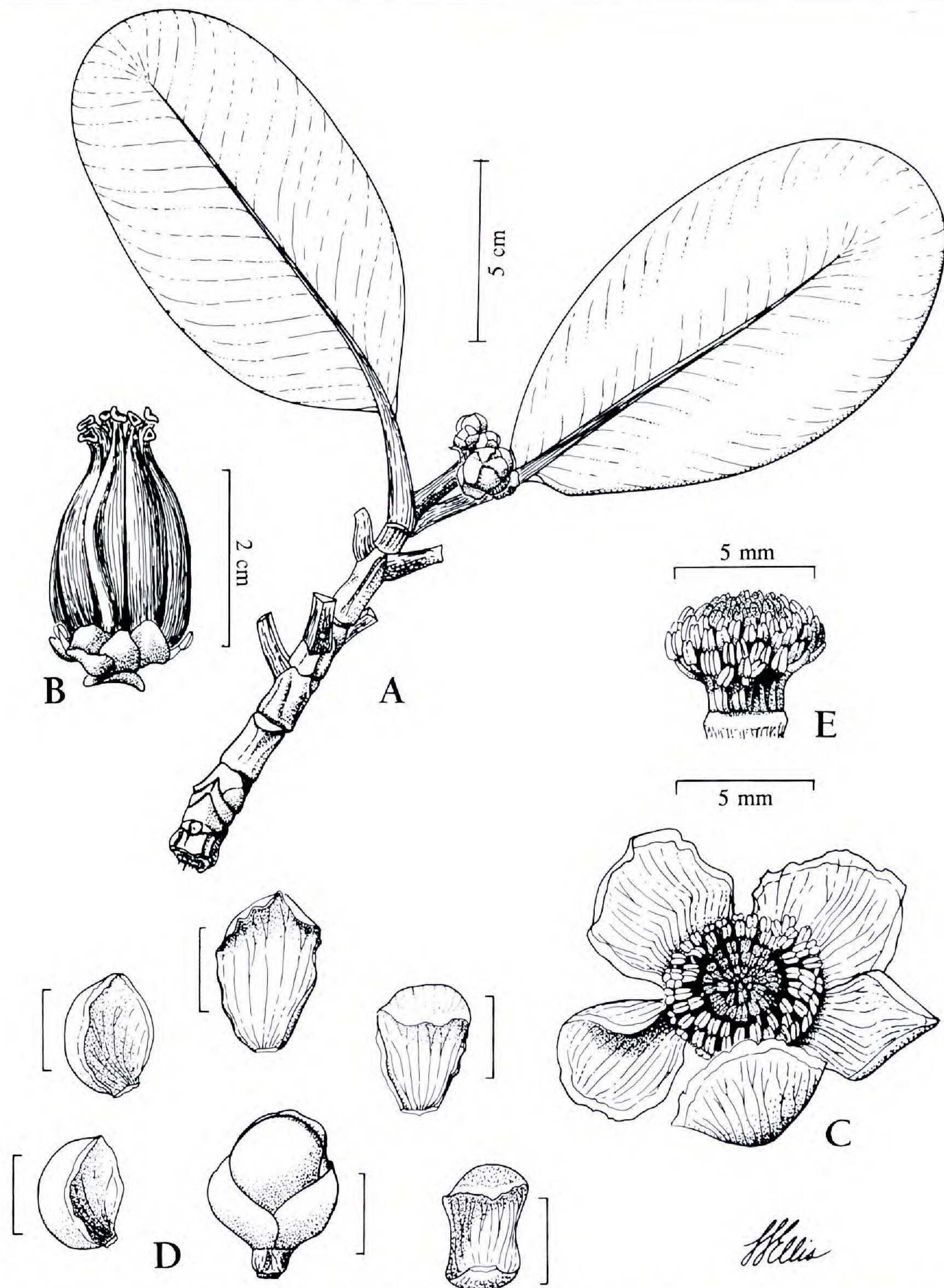


FIG. 5. *Clusia aymardii* Pipoly. A. Habit, showing cartilaginous leaves with broadly rounded bases and subterete petioles, erect inflorescence and sessile flowers. B. Fruit, showing costae. C. Staminate flower at anthesis, showing numerous stamens and somewhat clawed petals with hyaline, scarious margins. D. Staminate flower bud, showing sepals (on left), and petals (above and on right). E. Androecium, showing emarginate anthers. A, C-E, drawn from type; B, drawn from G. Aymard 5918. All unmarked scale bars represent 5 mm.

Glabrous, free-standing tree to 3 m tall; latex white, branchlets terete, 10–15(–22) mm diam., longitudinally ridged when dry. Leaves cartilaginous, the blades oblong elliptic, (10–)12–18 cm long, (5–)7–11 cm wide, apex very widely rounded to truncate, base obtuse to widely rounded and slightly inequilateral, nitid above, pallid below, costa raised above and below, secondary veins numerous, inconspicuous, latex canals, narrow, vein-like, margin entire, opaque; petiole subterete, (3–)3.5–4(–5) cm long, longitudinally ridged. Inflorescence erect, glomerate, (4–)8–12-flowered, peduncle essentially terete, 1–2 cm long; floral bracts 4, decussate, cartilaginous, oblate to depressed-ovate, (5–)8–10 mm long, 10–13 mm wide, apex obtuse, base subauriculate, carinate medially, margin scarious; pedicels obsolete. Staminate flower with latex canals not obvious in any perianth part; outer sepals 2, opposite, coriaceous, depressed-ovate, 7.7–8.4 mm long, 9.8–11.4 mm, wide, apex truncate, margin scarious, entire, inner sepals 5, contorted, coriaceous, obovate-spathulate, 9–12 mm long, 7.7–9.8 mm wide, apex broadly rounded, margin scarious, entire; petals 5, spirally arranged, chartaceous, 13.5–17.2 mm long, white, somewhat clawed; limb widely obovate, 7–8.4 mm long, 9.1–10.8 mm wide, apex truncate, base cuneate, with numerous longitudinal linear resin canals, the margin entire, undulate, hyaline, scarious, the claw 6.5–9.8 mm long, 3.6–4.2 mm wide; stamens numerous, 2.5–2.9 mm long, free; filaments prismatic, 1.5–1.8 mm long; anthers muticous, developmentally adnate to abaxial stamen surface, 0.8–1.1 mm long, distally highly recurved, emarginate at apex and base. Pistillode absent. Pistillate flower (in bud) like staminate but .sepals 7, the outer 2, decussate, oblate, 5 mm long, 8–10 mm wide, the inner 5, spiral, same shape, size and texture as in staminate flower; staminodes chartaceous, resiniferous, numerous, in one whorl, at times several con-nate in phalanges, anantherous, 6–8 mm long, 2–3 mm wide, apex muticous; pistil oblongoid, 5 mm long, 4 mm diam., styles absent, stigmas cuneiform, ca. 1.5 mm long, 1 mm wide. Fruit a 7-carpelled capsule, oblongoid, crimson, 3 cm long, 1.5 cm diam., strongly ribbed, the stigmas sessile, cuneiform, flat, persistent.

TYPE. VENEZUELA. BOLÍVAR: summit of Cerro Guaiquinima, falls at Río Szczerbanari (Río Carapó), 1–2 km upriver from Szczerbanari Falls, 05°44'04" N, 63°41'08" W, central part of mountain, 750 m, 20–25 Jan 1977 (stam. fl), J. Steyermark & G. C. K. & E. Dunsterville 113157 (HOLOTYPE: VEN!; ISOTYPES: F!, MO!, NY, US).

PARATYPES. VENEZUELA. BOLÍVAR: Dtto. Heres, Cerro Guaiquinima, Camp 2, 05° N, 63°00'W, 1,200 m, 7 Feb 1990 (stam. fl), B. Boom 9430 (BRIT, NY, VEN); central base of Guaiquinima-Tepuí, scrub forests along Quebrada Martínez, 85 km S of La Paragua, 06°04'N, 63°22'W, 500 m, 11 May 1987 (fr), G. Aymard 5918 (PORT); Mpio. Raul Leoni, Cerro Guaiquinima, ca. 15 km NE of Río Paragua, 05°43'N, 63°35'W, 800 m, Nov 1988 (pist. fl bud), Y. Fernández 275 (BRIT, PORT, VEN).

Distribution.—Endemic to Cerro Guaiquinima, state of Bolívar, Venezuela, at 750–1,200 m elevation.

Ecology and conservation status.—*Clusia aymardii* occurs only in scrub forests on the slopes and summit of Cerro Guaiquinima, and as an endemic, may be considered threatened.

Clusia aymardii is most closely related to *C. spathulaefolia*, but is easily recognized by the oblong to elliptic leaf blades with obtuse to broadly rounded bases and flat margins, the subterete, longer petioles, and thicker branchlets. While Cerro Guaiquinima is known to be poor in terms of numbers of endemic species (Pipoly 1992), *C. aymardii* is a remarkably distinct species.

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BOOK REVIEW

GRAHAM, LINDA E. 1993. *Origin of Land Plants*. (ISBN 0-471-61527-7, hbk.) John Wiley and Sons, New York. \$89.00. 287 pp. 189 figures.

Linda Graham's entire career had been devoted to research on the origin of embryophytes from algal progenitors. In the *Origin of Land Plants*, she summarizes and synthesizes not only her own outstanding research, but the history of the debate, the pertinent research by other workers, and further unresolved issues. Although anyone would be tempted to bias such a synthesis in favor of one's own favorite hypothesis, she had provided a balanced, almost detached, review of the questions of embryophyte origins.

The first three chapters provide background to the problem of embryophyte origin, including early Paleozoic environments, current research methods being applied, and the consensus that the Charophyceae are the closest algal relatives of land plants. The next three chapters examine the Charophyceae in detail and compare them to land plants. Three more chapters follow with in-depth discussions on the evolution of significant features such as the cytoskeleton, cytokinesis, origin of embryos' sporophytes, nutrient transfer regions, control or meiosis, phytochrome systems, and phenolic biosynthetic pathways. The final chapter recapitulates the ideas presented in the previous chapters.

The book is clearly aimed at advanced undergrads, graduate students and professional botanists. In the final chapter Dr. Graham reveals her hopes that the book (or least that chapter) will be used by authors of introductory texts to update the often mistaken view students have of plant evolution. Certainly I found the book, especially chapters 3, 7, and 10, to be of great help in preparing lectures for an introductory botanical survey course at Southern Methodist University.

The book is a welcomed addition to the modern botanical literature, and I recommend it for every botany professor and college library.—*Roger W. Sanders*.